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IN MEMORIAM

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# In Memoriam – Daniel Wu Fong (born December 1, 1954; died April 25, 2025)

David C. Culver[1]

1 *Department of Environmental Science, American University, 4400 Massachusetts Ave. NW, Washington D.C. 29916, USA*

Corresponding author: David C. Culver (dculver@american.edu)

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With the death of Daniel Wu Fong, the cave biology community lost one of its most vibrant and active members. Dan will be remembered not only for his ready wit, his infectious laugh, his optimism, but also for his probing intellect and a series of landmark papers on various aspects of cave biology, but most especially having to do with the heart of the neo-Darwinian paradigm, as Ernst Mayr, in a famous essay in 1973, put it, "nothing makes sense in biology except in the light of cave evolution." Beginning with his thesis on inheritance of quantitative morphological straits in the cave and spring amphipod, *Gammarus minus* to his recent work on the transcriptomes of cave and spring populations of *Gammarus minus*, he has demonstrated the centrality of natural selection in molding the morphology of cave animals.

Dan had a peripatetic early life. Born in the People's Republic of China, he was taken to an aunt in Hong Kong, who subsequently adopted him and moved to the San Francisco area, where Dan went to high school. He got his B.A. in Zoology at the University of California—Berkeley, an exciting time to be at Berkely, to put it mildly. After several years of working at the Midwest Research Institute in Kansas City, Dan enrolled as a master's student at the University of Oklahoma. These years had a profound impact on Dan, and it was here he developed his love of caves. After he received his M.S. in 1980, he came to Northwestern University with David Culver. Following the pioneering work of three American cave biologists—Thomas Barr, Kenneth Christiansen, and Thomas Poulson—who modernized the

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study of cave biology and brought it into the neo-Darwinian firmament, Culver, together with Thomas Kane, sought to provide a rigorous demonstration that natural selection, rather than genetic drift or organicism, was responsible for the morphology of the amphipod *Gammarus minus,* which occurs in springs and caves, with many cave populations showed a highly modified morphology of tiny eyes and reduced pigment. Dan's thesis was absolutely critical to this work. What he showed in his Ph.D. work [4], by an analysis of individual pair matings in the laboratory, was that indeed differences in eye size, antennal length, and overall size was genetically (i.e., heritable), rather than environmentally determined. This study became an integral part of the book length consideration of the role of natural selection in the evolution of cave inhabiting populations of *Gammarus minus* [13] as well as a review of regressive evolution in general in The Annual Review of Ecology and Systematics [14].

In spite of its importance, an analysis of heritability for any subterranean organism has never been repeated. Why? First, and most importantly, it is a monumental among of work, requiring development of rearing techniques, hundreds of individual pairings, as well as detailed morphological analysis. There were more technical reasons as well, involving, at least for *Gammarus minus*, the impossibility of matings of the same female with different males, the so-called half-sib analysis of heritability studies. In the longer term, the entire field of quantitative genetics, with the analysis of heritability by sibling studies, became much less important with the advent of molecular techniques, such as analysis of quantitative trait loci (QTL's) and transcriptomes (expression of genes into proteins). While his colleagues and mentors moved on to other questions and other systems, Dan stayed with *Gammarus minus* and developed new collaborations with molecular geneticists, especially David Carlini of American University, that allowed the use of these new molecular tools in the study of *Gammarus minus* [21,27,31,34]. Especially impressive was the demonstration, by transcriptome analysis, that selection on eyes in cave populations was widespread [35]. In addition to the molecular genetic analysis, Dan also expanded our knowledge of the biology of *Gammarus minus* [1,3,6], including trophic analysis using stable isotopes [32].

He expanded his work on *Gammarus minus* in several other directions. One was to champion *Gammarus minus* as a model system for studying evolution [29,39,43]. Few cave-dwelling species can be raised in lab [45], and fewer still can be successfully mated with surface dwelling populations. In fact, only a handful of such species exist and *Gammarus minus* was only one of three such species that were given special treatment in the second edition of Groundwater Ecology and Evolution, the research agenda setting volume, edited by Malard, Griebler, and Rétaux in 2023. A second expansion was his work on Organ Cave in West Virginia. Organ Cave and its associated resurgence were the subject of many of his studies on heritability and molecular genetics, and he also considered Organ Cave in a general ecological context, with studies of microdistribution and community structure [9,12,16].

While his study of *Gammarus minus* is the core of his scholarly contributions, he made significant contributions in several areas, especially conservation biology

and management. He devoted a lot of attention to the endangered isopod *Antrolana lira,* a groundwater dwelling species, distantly related to some groundwater isopods in Texas and hundreds of kilometers from any marine waters, the historical source of colonists. While much of this work was in the form of difficult to obtain reports to the U.S. Fish and Wildlife Service, he published a paper demonstrating that it was likely three species, not one, based on molecular genetic analysis. The evolutionary origin of *Antrolana lira* is unknown, but Dan, rather whimsically, suggested it came from a tidal wave when a meteor hit the Chesapeake Bay in Maryland in the late Eocene! He also contributed an important chapter on management of cave fauna in general in Van Beynen's book, Karst Management [25].

Dan made many important contributions to biodiversity of cave fauna, including new species descriptions [18,23], biology and natural history notes [16,19,20,40], and local and regional species lists and biogeographic analysis [8,10,17,26,28,36,37], mostly focused on the fauna of West Virginia caves. He has also had three species named after him:

- *Pseudotremia fongi* Shear 2008 (a millipede from Greenbrier County, WV)
- *Niphargus fongi* Fišer & Zagmajster 2009 (an amphipod crustacean from Slovenia)
- *Monolistra fongi* Prevorčnik & Verovnik 2010 (an isopod crustacean from Croatia)

At American University, he was unstinting in his support of graduate research and education, chairing the MS thesis committees of 18 students, most of whom did cave related projects. For five, their thesis work resulted in a publication—Ariel Aspiras [27], Natalie Hanson [24], Benjamin Hutchins [22], Shannon Knapp [16], and Mara Laslo [35]. He was a sought-after collaborator and even a glance at his bibliography shows many names of North American and European collaborators. Noteworthy are the numerous collaborations with speleobiologists working in the classic Karst. These include Helena Bilandžija [35,44], Tanja Pipan [17,40], and Maja Zagmajster [26,40].

Dan played a prominent role in the Karst Waters Institute, serving on its Board of Directors from 1991 to 1996, Treasurer from 1997 to 2007, and finally president from 2007 to 2012. He also founded the online journal **Speleobiology** in 2008 and served as editor until 2012. He was also very active in the National Speleological Society and received the Science Award in 2023.

Dan was outstanding in his ability both to ask probing questions about one's research and to ask more general questions. All of us who had the privilege of working with him were the recipients of this bounty. I would be remiss if I did not mention one of his most important social contributions—a co-founder of the District of Columbia Biospeleological Drinking (Discussion) Club (DCBDC). But, surely all of us who knew him remember most of all his infectious good humor, his positive attitude, and his wonderful laugh.

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